

Plant trait covariance and nonlinear averaging: a reply to Koussoroplis et al.

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Keywords

Nonlinear averaging, Jensen's inequality, intraspecific trait variability, plant diversity, plant–herbivore interactions, consumer–resource dynamics

In a previous paper, we re-analyzed data from 76 published studies on the relationships between plant trait levels and insect herbivore performance and found that variation in plant nutrients reduces insect herbivore performance via nonlinear averaging (Wetzel et al. 2016). In their insightful comment, Koussoroplis et al. (2019) affirm the importance of our conclusions regarding nutrients but argue that we underestimated the importance of plant defense variance.

Their first point is that reporting a mean effect size masked important negative and positive effects because opposite signs with similar magnitudes would average to zero. Koussoroplis et al. (2019) suggest we should have reported absolute values of effect sizes, or positive and negative effects separately. While these are valid suggestions, they do not change our results. Defense effect sizes were distributed unimodally with mean and mode near zero (Fig. 1), and calculating the absolute values produced a mode at zero and mean at 0.18, which represents a small effect (Cohen 1988; Rosenberg et al. 2013). Importantly, because absolute values follow a folded normal distribution – not

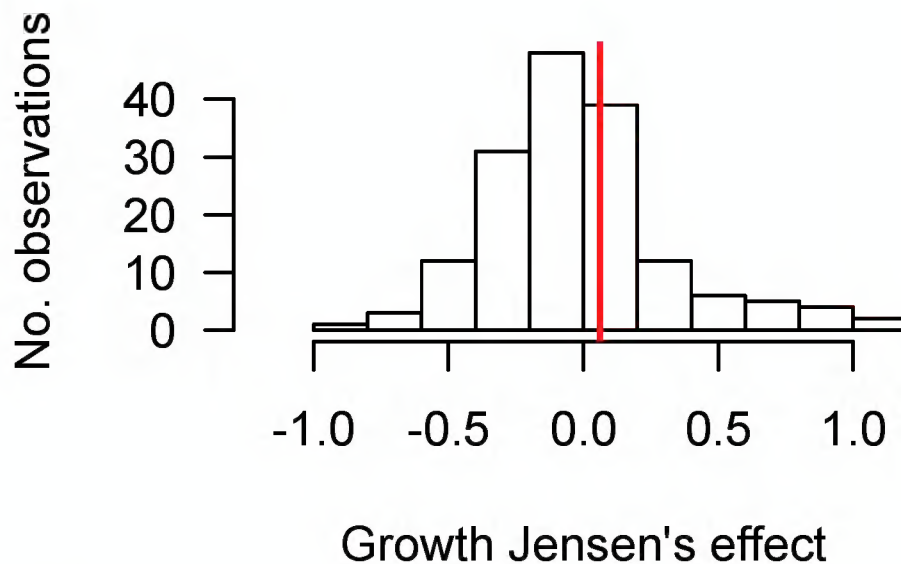


Figure 1. Frequency distribution of plant defense effect sizes. The vertical red line indicates the mean effect size calculated using a random effects meta-analysis model.

a normal distribution – we used a randomization test to show the mean was not significantly greater than zero ($P = 0.98$). Likewise, when evaluated separately, positive and negative effects had means not significantly different from zero ($P = 0.99$ and $P = 0.61$). These calculations affirm our finding that defense-performance relationships are truly linear on average – not just because of a fallacy of the averages.

The second point is that we considered defenses individually and ignored interactions between traits. This was necessary because of the scarcity of published experimental data on interactions. Of the 76 studies that met our search criteria, only nine examined interactions, and only one of those tested enough levels to quantify the multivariate nonlinearities that result from interactions. We fully agree that interactions have potential to make defense variance important. However, current data make it premature to conclude that we have underestimated the effects of defense variance on herbivores by ignoring trait interactions. As Koussoroplis et al. (2019) explain, the effect of an interaction on nonlinear averaging depends on (1) the strength of the interaction and (2) the correlation among the interacting traits at the relevant scale (Koussoroplis et al. 2017). Evidence for trait correlations is mixed across plant species (Agrawal and Fishbein 2006; Moles et al. 2013) and across genotypes within a species (Agrawal 2005; Johnson et al. 2009). When found, correlations are almost entirely under 0.5 in magnitude (Koricheva et al. 2004; Johnson et al. 2009), which would halve the effect of interactions on nonlinear averaging, all else being equal (Koussoroplis et al. 2017). Also, it is not enough to show that interactions and trait correlations are common across systems; for trait interactions and correlations to influence nonlinear averaging, they would have to be present in the same system, which is not always true. For example, Tao et al. (2013) show that cardenolide toxins interact with nitrogen in milkweed to influence monarch performance, but that cardenolides and N are not correlated.

In addition to trait interactions, there are also several other mechanisms that could lead defense variance to influence herbivores in ways we were unable to evaluate due to a lack of data. Variation in defense traits could prevent herbivores from physiologically

acclimating to host plants (Wetzel and Thaler 2016), increase foraging costs (Schultz 1983), or present an inconsistent target for natural selection (Whitham and Slobodchikoff 1981). Indeed, Pearse et al. (2018) recently showed that variance in xanthotoxin, a toxic furanocoumarin found in species in the carrot family (Apiaceae), suppresses the performance of cabbage looper (*Trichoplusia ni*) caterpillars via the physiological costs or constraints associated with physiological acclimation to a temporally varying defense, and these effects differed from those predicted by nonlinear averaging alone.

We join Koussoroplis et al. (2019) in calling for more research into the consequences of defense trait variance, covariance, and interactions. Resolving these effects will greatly advance our understanding of the ecological consequences of plant trait diversity.

AUTHOR CONTRIBUTION

Designed and wrote the manuscript: WW, KH, RM, HM, KR.

Table 1.

Authors	Contribution	ACI
WW	0.32	1.882
KH	0.17	0.819
RM	0.17	0.819
HM	0.17	0.819
KR	0.17	0.819

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